

THE SLAVE-RAIDS OF *HARPAGOXENUS AMERICANUS*.

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The observations here recorded were made at the American Museum of Natural History's Station for the Study of Insects at Tuxedo, N. Y. Through the courtesy of Mr. Frank Johnson of New York City the author was enabled to spend the summer of 1926 at the Station. To Mr. Johnson and to Dr. Frank E. Lutz, whose encouragement and support greatly facilitated this work, the writer wishes to express his sincere thanks. After the manuscript had been prepared it was learned that Dr. Sturtevant had made a number of observations about the same time on *Harpagoxenus* colonies found in New Jersey. I have had the opportunity of reading Dr. Sturtevant's manuscript and his results and mine amplify each other with very little repetition. In several cases observations have confirmed hypotheses in a remarkable manner, all the more striking in that neither of us knew of the work of the other. Dr. Wheeler has, therefore, suggested the simultaneous publication of the articles as they were originally prepared.

In 1893 Pergande found, near Washington, D. C., a mixed nest composed of *Leptothorax curvispinosus* (Fig. 1. B), and an unknown ant to which Mayr subsequently gave the name *Tomognathus americanus* (Fig. 1, A). Later the generic name was changed by Forel to *Harpagoxenus*, the specific name remaining unaltered. Besides the type specimens of *H. americanus* Mayr had a few others accidentally taken by Schmitt while collecting beetles at Beatty, Pa. During the next twelve years there are no further records of this ant until, in 1905, Dr. Wheeler discovered, near Bronxville, N. Y., three small mixed colonies of *H. americanus* and *L. curvispinosus* nesting in hollow elder twigs. The next observation on this rare insect came twenty years later when Sturtevant, during the summer of 1925, found on Naushon Island (Woods Hole) a mixed *Harpagoxenus*—*L. curvispinosus* colony inhabiting an oak gall.

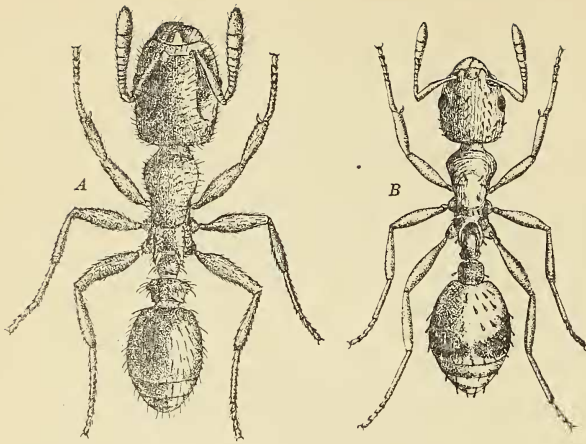


Fig. 1. A, worker of *Harpagoxenus americanus*; B, worker of *Leptothorax curvispinosus*, after Wheeler.

During the past summer I found a number of nests of *H. americanus* near Tuxedo, N. Y., and was fortunate enough to see these ants engaged in slave raids. In all but one nest the slave ant was *L. longispinosus*. The remaining colony contained slaves of both *L. longispinosus* and *L. curvispinosus*, a condition parallel to that described for the European *H. sublaevis*, which enslaves both *L. acervorum* and *muscorum*. Dr. Wheeler postulated that such colonies should occur, since he found a queenless *longispinosus-curvispinosus* colony in the vicinity of the *Harpagoxenus* nests. However, since he did not think *H. americanus* a dulotic ant, he considered the colony as one which needed only the advent of a deälated *Harpagoxenus* queen to form a mixed colony containing two species of slaves. For reasons to be subsequently given I would consider Dr. Wheeler's mixed *Leptothorax* colony as a remnant, originally formed by dulosis, from which the *Harpagoxenus* had migrated or been killed off while raiding.

Before taking up the discussion of *H. americanus* it seems advisable to briefly outline the ethology of the European species. *H. sublaevis* has been known since 1848, and since that time a number of observations have been made on its habits. It appears to have a wider distribution than its American cogener, for it has

been taken in Finland (Nylander), Denmark (Meinert), Sweden (Stolpe and Adlerz), Saxony, West Prussia, Bohemia (Viehmeyer) Kärnten, Austria (Wolf), and the Swiss Engadine (Emelius). In this last location it occurs at an altitude of 1600-1700 meters. The pioneer observer of *sublævis* was Adlerz, who in 1896 conducted numerous experiments on these insects in artificial nests, supplemented by observations in the field. He found that in the mixed colonies the slave ant was usually *L. acervorum*, occasionally *L. muscorum* and rarely *L. tuberum*. Normal dejected *Harpagoxenus* queens were never present, their place in the colony being taken by the ergatoid female, a wingless worker-like insect possessing ocelli and a *receptaculum seminis*. Adlerz further showed that the *sublævis* workers, if forced to do so through the absence of slaves, are able to feed themselves but do not care for the brood. This is normally tended by the slaves who feed the larvæ with regurgitated material and fragments of insects. This last observation was later confirmed by Viehmeyer, who amplified the work of Adlerz by discovering, near Dresden in 1906, the true winged queens of *sublævis* which Adlerz had supposed did not exist. Viehmeyer's observations ('08) show that the actions of a *sublævis* female in founding a colony closely parallel those of *sanguinea* queens. After the entrance of the parasitic female into the *Leptothorax* nest the workers attack her, but are eventually killed or driven away by the larger insect who then takes possession of the nest and brood. Adlerz had previously observed similar actions of the ergatoid females and had concluded that *sublævis* customarily obtains its slaves in this manner. Such dispossession was thought to be fundamentally different from the raids of the amazons and sanguinary ants, who, after the pillage of the strange nest, return to their own with the plundered brood. Both Adlerz and Viehmeyer saw the "raids" of *Harpagoxenus*, if by this term we may translate the *eröfringstag* of the former writer and the *Raubzug* of the latter. Unfortunately both these investigators interrupted the proceedings by disturbing the nests, with the result that it is impossible to tell from their observations whether they witnessed a true raid or the dispossession of *Leptothorax* nests by the *Harpagoxenus*. Indeed, Adlerz considered

that this last was what he had seen, but Viehmeyer seems to have interpreted the two forays which he discovered as true raids. Moreover each found mixed colonies which contained slaves of both *L. acervorum* and *L. muscorum*. Since the possibility that such colonies could have been formed by dispossession is very remote, these investigators concluded that *H. sublaevis* must make dulotic raids. It is gratifying to be able to supplement their observations with others on the dulosis of *H. americanus*.

The slave raids of *Harpagoxenus* show none of the organization and spirit so characteristic of those of *Polyergus*. They fall far short even of the lesser degree of cooperation exhibited by *F. sanguinea*. Nevertheless they are of great interest, since they appear to be the last manifestation of a vanishing character. They show the decay of dulosis and foreshadow a state of abject parasitism. During the progress of a raid the *Harpagoxenus* workers and their slaves cluster about the entrance of their nest in a manner suggestive of *Polyergus*, but with this the similarity ends. There is no rapidly moving phalanx of raiders, no concentration about the entrance of the raided nest, no frantic activity to enlarge the entrance. The *Harpagoxenus* leave their nest singly and amble awkwardly and uncertainly to the nest of their victims. Only once did I see more than one *Harpagoxenus* leave the nest at the same time. On one occasion a column of three departed for the *Leptothorax* nest. However, this column broke up almost at once and was, I believe, purely fortuitous. On arriving at the *Leptothorax* nest the *Harpagoxenus* wastes no time in preliminaries but enters at once. Having secured a larva or pupa it emerges as quietly as it entered and returns with its burden to its own nest. Quite often they lose their way and I have seen a number of them captured by small spiders while raiding. The action of *Harpagoxenus* after it enters the raided nest could not, of course, be followed in the field. However, observation of ants in artificial nests show that the brood is obtained by force and not by stealth, although indeed, the action of the *Leptothorax* during a raid furnishes ample evidence that this is the case.

The nest which yielded most of the observations on the



slave-raids was ideally situated for such work. It was in a crevice in one of the many out-jutting ledges of rock which studded a slope above a small pond. Jammed into the crevice was a small flake of stone which formed a little shelf on the perpendicular face of the ledge, and between this flake and the solid rock the nest was constructed. The entrance had been enclosed by a carton of lichens, perforated in the center by an almost circular aperture. Eleven feet away under the bark of a small log which rested on the ledge was the nest which the raiders visited. Between the two nests the ledge was bare except for large black lichens and occasional leaves and fragments of bark. The progress of the raiders could therefore be followed with the greatest ease, an important consideration when dealing with small, slowly moving insects.

The first raid was observed on August 4th. Arriving at the nest at 3:00 P. M. I noticed a crowd of *Leptothorax* and *Harpagoxenus* about the entrance. At 3:02 a *Harpagoxenus* arrived with a pupa. Another at 3:04. In both cases the *longispinosus* workers crowded about the returned raider apparently attempting to relieve it of its burden. A third pupa was brought in at 3:08 and carried directly into the nest by the *Harpagoxenus*, which turned and backed into the entrance pulling the pupa in after it. At 3:25 a *Harpagoxenus* arrived with a callow. Another with a pupa at 3:26. In each case the raider entered the nest with its burden in the manner just described. During transportation the pupæ are held in such a way that they project forward and upward in front of the head of the raider.

The log in which the raided nest was located was small and badly decayed. The bark had loosened with the decomposition of the underlying wood and, as was later determined, just under the bark in a roughly oval excavation was the raided nest. To this the *Harpagoxenus* gained access through a rupture in the bark several inches away. The actions of the raiders on arriving at the log were somewhat disconcerting. They entered as nonchalantly, if I may be pardoned an anthropomorphic term, as though it had been their own nest. However any doubts as to the nature of their visit were quickly dispelled by the action of the *Leptothorax*. About ten inches from the point

where the raiders entered a group of *longispinosus*, with part of the brood, had collected on the surface of the bark. They were huddled above the brood or moving uneasily nearby. In the group were several males. The importance of this observation cannot be minimized. It is proof positive that the actions of the *Harpagoxenus* were dulotic and not migrational. It removes the possibility that the nest in the log was a remnant of the mixed nest in process of transportation to a new site. It shows that the *Leptothorax* were aware of the presence of the raiders and, being unable to prevent the pillage of their nest, had resorted to flight to save the brood. Coupled with the actions of the raiders it establishes their dulosis in a manner which seems incontrovertible.

Additional evidence of a less conclusive nature was obtained by an examination of the raided nest. This was made on August 9th, after a heavy thunderstorm had put an end to the raids. The *Leptothorax* colony was in no respect a remnant. No *Harpagoxenus* were present. There were about forty *longispinosus* workers, a brood consisting largely of larvæ, and a dozen virgin queens. The old queen I could not find. It is entirely likely that she had perished during the raid, but in any case the presence of the virgin queens is a guarantee that the colony had been queenless for only a short time, if at all. Alderz's observation that sexual forms of the slaves are sometimes present in mixed colonies of *H. sublavis* invalidates what might be otherwise considered additional conclusive evidence of the individuality of the raided nest. However the character of the *Leptothorax* colony is at least not contradictory to the conclusion reached above.

I shall cite one further field observation before taking up those made on ants in artificial nets. It may perhaps serve to impress the reader with the degenerate nature of the dulosis of *Harpagoxenus*. On August 5th I arrived at the mixed colony at 2:00 P. M. The entire ledge was in the shade and no ants were outside the nest, although I could see the head of one in the entrance. During the next three quarters of an hour a few *Leptothorax* left the nest and wandered about on the ledge nearby. During this time also the shadow had shifted, so that when at

2:45 the first *Harpagoxenus* emerged the ledge was in the bright sunlight. After a short period of aimless wandering the *Harpagoxenus* started in the direction of the raided nest. Its progress was slow and uncertain, and on several occasions it became lost, to judge from its haphazard movements. It entered the *Leptothorax* nest at 3:14, having required twenty-nine minutes to cover 3.35 meters. Five minutes later it emerged with a callow and began to retrace its steps. In so doing it passed close to a *longispinosus* worker. The later drew back at its approach and then stood perfectly quiet until the raider had passed, an action which I subsequently observed many times in the artificial nests. Despite the added burden the *Harpagoxenus* completed the return trip in twenty-two minutes, entering its nest at 3:42. Neglecting the preliminary movements after its emergence from its nest, and deducting the five minutes spent in the raided nest, the entire trip of about 6.7 meters had been completed by the *Harpagoxenus* in fifty minutes. This gives it an average speed of 13.5 cm. per minute. Compare this with Dr. Wheeler's observations ('10) on the speed of *Polyergus* when raiding, viz: 1.3 meters per minute. It is true that *Harpagoxenus* is a small ant, scarcely a third the length of *Polyergus*, yet its smaller size will hardly account for its discrepancy in speed. I recently had the opportunity to study the rate of movement of *Iridomyrmex humilis*, a smaller ant than *Harpagoxenus*, and found that under optimum conditions it moved at the rate of approximately 2.75 meters per minute. Size, then, has little to do with the activity of an ant. If, as seems altogether likely, we can assume the correctness of Dr. Wheeler's postulate, ('07) that the ancestors of dulotic ants were active, predatory insects; if from this condition dulosis arose as a refinement of active predatism; then we must regard an ant which, though a raider, is slow and clumsy of movement as one in which the dulotic instincts are nearing extinction.

We now take up a series of observations upon ants in artificial nests, which are of interest in that they suggest what takes place when the raiders first enter the nest of their victims. On August 20th, while collecting in a damp wood, Mr. Brandt Steel called my attention to what I at first took to be a mixed colony

of *Harpagoxenus* and *L. curvispinosus*. The nest was situated in a hollow twig that rested on a moss-covered rock. The open end of the twig had been plugged with a beautiful lichen carton with the customary circular aperture in its center. On the outside of the twig a group of the yellow *curvispinosus* clustered about a *Harpagoxenus* worker, while on the rock immediately below was a similar group. The entire colony was easily collected, placed in a handkerchief, and subsequently transferred to a plaster observation nest. On splitting the twig two more *Harpagoxenus* workers were found. Once the nest was installed in the observation nest it became apparent that I had misjudged the situation. The only queen present was that of the *Leptothorax*. Moreover under the binocular I could see the *curvispinosus* workers clinging with locked mandibles to the legs and antennæ of the *Harpagoxenus*. Here was no mixed colony but a number of raiders, fiercely resisted by the *curvispinosus*. That the latter had suffered in spite of their superior numbers was evident from their missing legs and antennæ. While I was watching, one of the *curvispinosus* maneuvering for a grip on the antenna of the *Harpagoxenus* had both its own antennæ bitten off when it came within reach of the intruder's jaws. Three of the four *Harpagoxenus* workers were thus surrounded. The fourth had found a shelter under a piece of leaf mould. Here it remained coming out only to drive away any *curvispinosus* that approached its refuge. By next day the *curvispinosus* had established themselves in a small cavity in the plaster at one end of the nest. The brood had been carried inside and the entrance partially blocked by vegetable detritus. During the night two of the *Harpagoxenus* workers had succumbed to the attacks of the *curvispinosus* and a third seemed badly crippled. The remaining *Harpagoxenus*, in all probability the one who had stayed under the leaf mould, was now surrounded by three *curvispinosus* workers which had fastened their mandibles on its legs and antenna. It made no efforts to extricate itself during the entire day but must have succeeded in doing so during the following night, for on the morning of the 2nd, it was wandering about the nest apparently uninjured. At this time there were nine dead *curvispinosus* workers in the nest.



At 1:37 P. M. the *Harpagoxenus* entered the little cavity in which the *Leptothorax* had placed their brood. Thirty seconds later the *curvispinosus* queen came hastily out and ran to the opposite end of the nest. After another thirty seconds a *curvispinosus* worker emerged with a pupa. This worker was followed by the *Harpagoxenus* for a short distance, but the latter quickly returned to the cavity. One minute later it appeared in the entrance to the cavity with a *Leptothorax* worker in its mandibles. This it dropped outside the cavity and immediately reentered. A general disturbance now pervaded the *Leptothorax*. An exodus of those in the cavity, many of them carrying pupæ, was followed by a spread of the excitement to the workers in the nest, who ran about in a confused and terrified manner. A few bold individuals remained at the entrance of the cavity and two ventured inside long enough for each to recover a pupa. A third worker who attempted to enter was apparently seized by the *Harpagoxenus*, for it disappeared into the cavity with startling suddenness and did not come out again.

At 2:00 P. M. the *Harpagoxenus* began a series of manœuvres which can best be described as "reconnoitering." At first it thrust only its head out of the entrance of the cavity and waved its antennæ about. At such times any *curvispinosus* near the cavity rushed away as though in terror. After about forty minutes of this behavior, it began making short sorties from the cavity. At first it hardly more than emerged, returning at once, but after twenty minutes it began to extend its reconnoiters. Twice during these sorties the *Harpagoxenus* attacked and injured a *curvispinosus* worker. In both cases this was done in a deliberate and spiritless manner. Most of the *curvispinosus* workers who chanced to encounter the intruder ran from it and were not attacked. When it left the cavity at 3:40 a change seemed to come over the *Harpagoxenus*. It no longer lumbered about the nest in its customary manner. Its movements were quick and active. During the next thirty-two minutes the *Harpagoxenus* attacked and injured eight *curvispinosus* workers with a ruthlessness and a "mordlust" that would have done credit to *Polyergus*. The victims were bitten in the thorax and abdomen and left in a dying condition on the floor of the nest. Twice



during the absence of the *Harpagoxenus* from the cavity a *curvispinosus* entered and secured a part of the brood, and once the raider returned in time to drive away two others who were about to enter. During the foregoing period most of the *Leptothorax* had collected in two groups on the floor of the nest, the larger of which contained the queen and the majority of the brood carried out of the cavity. The *Harpagoxenus* now began to pass close to the *curvispinosus*. At 4:19 it approached the smaller group and attacking the workers, drove them away from the brood. This it examined with great care, touching the larvæ and pupæ with its antennæ. Two *curvispinosus* workers which attacked it in a half-hearted manner were quickly driven away. To my surprise it left the brood unmolested and turned to the larger group of *Leptothorax* which was now in great confusion. Some of them the *Harpagoxenus* drove away, attacking so vigorously two workers burdened with pupæ, that the pupæ were abandoned and their bearers put to flight. It then attacked a *curvispinosus* callow and soon afterwards bit off the antennæ of a worker. At 4:28 it returned to the cavity having taken no further notice of the brood. At this point the observations were interrupted for an hour and a half. When I returned the *Harpagoxenus* had left the cavity and had been seized by three *curvispinosus* workers. All of its former spirit and activity was gone, nor did it ever again manifest these characteristics. It lay supine and unresisting on the floor of the nest, its antagonists attached to its legs with locked mandibles. This was the condition at 10:00 P. M. However by next day it had freed itself and, to judge from the diminished brood of the *Leptothorax*, had carried a number of larvæ and pupæ into the cavity. At 11:17 A. M. it emerged, secured a pupa and returned with it to the cavity. The disorganization of the *Leptothorax* was complete. Twenty dead or dying workers were scattered about the nest. The queen lay on one side apparently dead. The remaining workers moved aimlessly about, a few carrying pupæ or larvæ. They no longer resisted or ran from the *Harpagoxenus* but stood perfectly quiet when it approached, and even allowed it to touch them with its antennæ. by the following day the *Harpagoxenus* had obtained practically all of the *curvispinosus* brood. Only five larvæ and pupæ remain-

ed outside the cavity. During the next night the *curvispinosus* recovered a part of their brood but this was again taken by the *Harpagoxenus*. This see-saw possession of the brood continued until September 3rd., when it was ended by the death of the *Harpagoxenus*. At this time there were eight *curvispinosus* workers still alive. They immediately occupied the cavity and resumed the care of the brood.

Any interpretation of the facts just described may be criticized on the grounds that the ants were captive insects placed in artificial surroundings. I am convinced that their actions may be explained on just such a basis, viz: that they were captives, unable to leave the artificial nest. There can be little doubt that the actions of the *Harpagoxenus* constitute a "dispossession" of the *Leptothorax* of their nest and brood. Nevertheless this cannot be regarded as the founding of a mixed colony. With this in mind I examined the four *Harpagoxenus* individuals with the greatest care and can positively state that not one of them was an ergatoid female, if one may judge by the absence of ocelli or a female type of gaster. Under such circumstances the most plausible explanation is that of an interrupted raid. A condition making the return of the raiders to their own nest impossible, in this case confinement in the artificial nest, is, I believe, the reason for such occurrences. I have already given reasons for believing that the vestigial dulosis of *Harpagoxenus* makes its raids, even under the most favorable circumstances, very precarious. The surroundings of the nest from which the raids described above took place were as nearly ideal as could have been wished. The distance between the two nests was comparatively short. The smooth rock surface with its scattered lichens offered a minimum of obstructions and a substrate which facilitated the progress of the raiders. Yet even here the *Harpagoxenus* had difficulty in finding their way to and from the raided nest and frequently lost their way. Under the less favorable conditions of terrain which usually surrounds the colonies the chances for a successful raid would be greatly lessened. The initial entry into the raided nest is, as the above observations show, a difficult matter requiring much time. During the interval, perhaps several days, from the advent of the first intruder

to the successful defeat of the defenders of the nest, there is ample time for altered external conditions. A heavy thunder shower might completely change the character of the ground between the two nests, efface any scent trails present, and render the return of the raider to its own nest extremely difficult or impossible. Under such circumstances there would result a mixed nest containing no queen but *Harpagoxenus* and *Leptothorax* workers. I found one such nest during the past summer and two of the nests which Dr. Wheeler discovered near Bronxville were of this character. It seems likely that the development of the ergatoid females in the European *sublaevis* may have come about as a response to frequently interrupted raids. An insect of this type, able to participate in a raid and equally able to function as a queen, should a return to its own nest become impossible, is at least a logical outcome of such conditions.

An enumeration of all the mixed colonies found during the past summer will be given here, together with such observations as have not been already recorded.

No. 1, found Aug. 4th, is the colony from which the raids took place. Since it was never disturbed an accurate count of the number of ants present cannot be given. It was, however, a comparatively large colony and I should estimate that it contained at least a dozen *Harpagoxenus* workers and ten or twelve times that number of *L. longispinosus* slaves.

No. 2, discovered on Aug. 6th, was the largest colony of any that were seen. It was under a stone on one of the ledges about thirty-five meters to the west of No. 1. Since the nest was almost entirely surrounded by an area of perfectly bare rock it was an easy matter to collect the whole colony. Stragglers that escaped the initial transfer were picked up with a camel-hair brush and placed in the artificial nest. I am certain that not more than half a dozen ants escaped. The colony contained a normal *Harpagoxenus* queen with vestiges of wings, 17 *Harpagoxenus* workers, 30 *L. curvispinosus* workers, 206 *L. longispinosus* workers 2 *longispinosus* males and considerable brood, most of which subsequently proved to be *Leptothorax*. The *Harpagoxenus* workers were very inactive, rousing themselves only to solicit

food from their slaves. The *Leptothorax* workers spent much time diligently licking their lethargic masters.

No. 3 can hardly be considered a mixed colony, for as such I designate the *L. curvispinosus* nest attacked by the four *Harpagoxenus* raiders. It was found Aug. 20th, and is included here for the sake of clarity.

No. 4 was taken on Aug. 24th. It was located under a small flake of stone on the top of a boulder about eight meters from the spot where No. 3 was discovered. It contained a normal, deŕalated *Harpagoxenus* queen, 11 *Harpagoxenus* workers, 113 *L. longispinosus* workers and a fair amount of brood. I feel sure that the raiders found in No. 3 came from this nest, but experiments to prove this, while not invalidating the opinion, gave inconclusive results. Six *Harpagoxenus* males were produced in this colony after its transfer to an artificial nest. These are so different from the insect figured by Alderz ('96) as the male of *H. sublaevis* that, were it not for his statement that he observed *Harpagoxenus* males in copulation with ergatoid females, it would seem likely that he had described aberrant males of *Leptothorax*. A figure of a *Harpagoxenus* male, together with a description is given at the end of this paper.

No. 5 was found on Aug. 30th., in dry, fairly open woods. The colony was under a flake of stone on the top of a boulder. Not wishing to disturb it I removed the covering stone only long enough to make certain of the presence of the *Harpagoxenus* queen, and to count the *Harpagoxenus* workers, of which there were twelve. I did not attempt to count the *longispinosus* slaves but would estimate that there were about a hundred.

No. 6, a small queenless colony was also found on Aug. 30th., about fifteen meters from No. 5. It consisted of two *Harpagoxenus* workers, ten *L. longispinosus* workers and a small brood of a dozen or more larvæ. When the stone covering the nest was removed both the *Harpagoxenus* and the *longispinosus* seized the larvæ and attempted to move them out of danger. I am of the opinion that this nest represents a *L. longispinosus* colony "dispossessed" by raiders from No. 5, who for some reason were unable to return to their own nest.

No. 7 was found on Sept. 3rd., about seventy-five meters



to the west of No. 5. It was plainly an incipient colony containing a normal deälated *Harpagoxenus* queen, one *Harpagoxenus* worker and thirty-five *longispinosus* slaves and a large brood composed entirely of larvæ. The queen was subsequently found to lack the last pair of legs, only the stumps of these remaining.

This mutilated condition was also true of a deälated *Harpagoxenus* queen which was taken on Aug. 3rd. This insect, which was crawling over a stone when discovered, lacked the left antenna and one leg on the left side. It seems likely that it had been repulsed in an attempt to enter a nest of *Leptothorax*, since there were two fairly large *longispinosus* colonies about three meters from the stone where the *Harpagoxenus* queen was found. A most careful search failed to reveal any mixed colony in that vicinity.

As may be seen from the foregoing descriptions *H. americanus* presents one striking contrast to the European species. Normal winged queens are the general rule with *americanus* instead of the ergatoid females which usually take their place in *sublævis*. The ergatoid form seems to be as rare in the colonies of *americanus* as are the winged queens in those of *sublævis*. I have never seen an ergatoid female in any of the colonies thus far observed.

While much remains to be done it is now possible to sketch the ethology of *H. americanus*; a hasty sketch to be sure with many missing features hypothetically supplied, but at least a beginning. In this picture we see the fertilized *Harpagoxenus* queen entering a *Leptothorax* nest by force. Having driven away or killed the original owners of the brood she appropriates this, tends it and is in turn tended by the resulting *Leptothorax* workers, until in time there arises a mixed colony. When the colony is well established the dulotic instinct manifests itself in the *Harpagoxenus* workers. These gain entrance to some *Leptothorax* nest after a long struggle in which their greater hardiness and superior size finally enables them to kill or intimidate the *Leptothorax* workers. If the external conditions are favorable the raid is carried to a successful conclusion and the brood of the pillaged nest is carried back to the mixed colony. If the



return of the raiders is rendered impossible then a fragmentary mixed *Harpagoxenus-Leptothorax* colony results.

The phylogeny of *Harpagoxenus* has been a matter of considerable speculation. The development of its raiding habits, a point formerly much disputed, is now agreed as paralleling that of *Polyergus*. Viehmeier ('21) eventually concluded that his hypothesis of the lestopibiotic derivation of the raids of this ant was untenable and accepted the above explanation. On the other hand, there has never been any doubt of the close morphological affinities of *Harpagoxenus* to *Leptothorax*. *L. acervorum* (subgenus *Mychothorax*) is considered as closely related to, or identical with the ancestral form. It is generally believed that the parasitic ants (intraspecific parasitoids) have been derived from those species which they parasitize. (Wheeler '19). Occasionally when the parasitic relation has been of long standing the original host may have become rare or extinct and have been replaced by another closely related to it. The relation of *Harpagoxenus* to its slaves clearly illustrates both these points. The resemblance between the European *H. sublavis* and *L. acervorum*, its usual host, is close. On the other hand *H. americanus* parasitizes either *L. longispinosus* or *curvispinosus*, neither of which it particularly resembles. This is exactly what we should expect from the distribution of the host species. *L. acervorum*, a dominant ant in the European palæartic fauna, is rare in North America. The dominant nearctic forms in this country are *L. longispinosus* and *L. curvispinosus*. It would be expected that the American *Harpagoxenus* would have adopted these forms in place of the rare *acervorum*.

In the study of phylogenetic relationships the males play an important part because of their morphological stability. Since the males of *H. americanus* have been hitherto unknown it seems advisable to devote a brief survey to the phylogeny of this ant. Through the kindness of Dr. Wheeler I have been enabled to examine material in his collection, and on this the following comparisons were made. We should expect morphological similarities to be most manifest in the males of the two genera and least apparent in the workers. Nevertheless even the latter exhibit a number of significant features in common. The work-

ers of *L. acervorum* and *Harpagoxenus* both have eleven-jointed antennæ. The importance of this lies in the fact that the subgenus *Mychothorax*, to which *acervorum* belongs, is the only one of the holarctic subgenera of *Leptothorax* which exhibits this characteristic. Furthermore, in both *Mychothorax* and *Harpagoxenus* there is an impressed mesoepinotal suture. Since the combination of these two characters is the criterion by which *Mychothorax* is separated from all the other subgenera in the group, their occurrence in *Harpagoxenus* leaves little room for doubt as to the close relation of the two genera.

The similarity between the males of *H. sublævis* and *L. acervorum* was close enough to confuse even such a careful observer as Adlerz. (96). Unfortunately it has not been possible to examine the male of *sublævis* but a comparison of Adlerz's figure with the male of *acervorum* showed differences which are rather surprising in the light of that author's statement. In *H. americanus* there are even greater differences. Nevertheless these insects show a sufficient number of similar characters to justify the view that *Harpagoxenus* has been derived from *Mychothorax*. The males of both genera have twelve-jointed antennæ and in *H. sublævis* the shape of the joints is almost identical with that of *L. acervorum*. Curiously enough except for the number of joints, the antenna of *H. americanus* resembles that of *L. longispinosus* rather than *acervorum*. The mandibles of *H. sublævis* are similar to those of *L. acervorum* in that they are toothless and so short that they do not meet. The mandibles of *H. americanus* are longer, toothed and mucronate at the tip. In regard to petiolar structure *H. americanus* more closely approaches *L. acervorum* than does *sublævis*. Neither of the former possess the ventral tooth which arms the second node of the petiole in *H. sublævis*. It is interesting to note that the second petiolar node in *L. acervorum* is somewhat expanded laterally, since the squamiform second node is a marked characteristic of *Harpagoxenus*. Allowing for the minor variations which occur within the species, the anterior wing venation in the males of the two genera is practically identical. The hind wings of *H. americanus* are veinless, but those of *sublævis* and *acervorum* are correspondingly veined.

From the foregoing consideration it is clear that *H. sublævis* shows closer affinities to *L. acervorum* than does *H. americanus*. This may be correlated with the habits of the two slave-makers. *Sublævis* has apparently always lived with the host from which it was derived and has therefore changed only slightly. On the other hand, *americanus*, adopting new hosts, has diverged to a greater extent from the ancestral type.

In conclusion is given a description of the male of *H. americanus* (Fig. 2.)

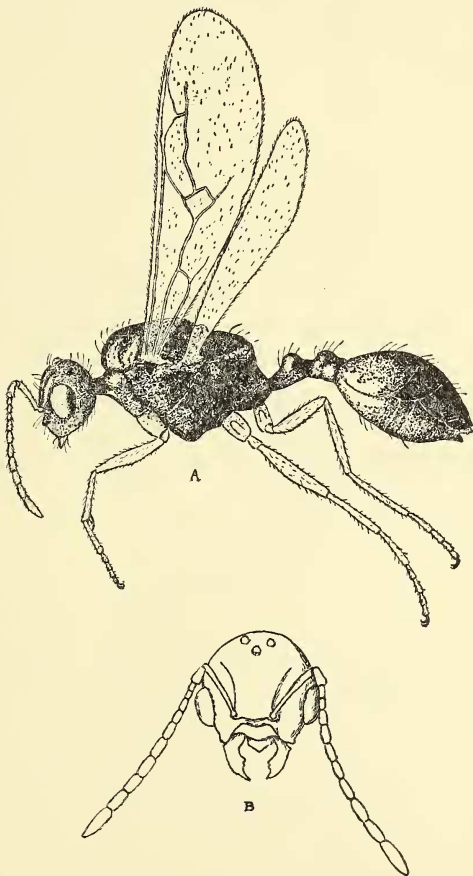


Fig. 2. A, male of *Harpagoxenus americanus*; B, head of same.

Length: 2.7 mm.

Color: head, thorax and abdomen brownish black; antennæ and legs very pale, almost transparent in fresh specimens.

Head rugulose with numerous erect hairs. Thorax feebly rugulose, somewhat glabrous, and with fewer hairs. Abdomen glabrous with sparse erect hairs. Antennæ 12-jointed. Funiculus without a distinct club but the joints gradually increasing in diameter towards the tip. First funicular joint pyriform, much broader than those immediately succeeding it. Second and third funicular joints cylindrical and distinctly shorter than the adjacent joints. The following joints sub-oval and gradually increasing in length towards the tip. Scape one quarter the length of the funiculus. Scape and funiculus clothed with a short erect pubescence. Antennal scrobes much shallower than in female and worker, but distinct. Mandibles long and narrow, feebly toothed and sharply mucronate at the tip. Neck long and flattened dorso-ventrally.

Anterior face of mesonotum abruptly projecting above pronotum. Mayrian furrows strongly impressed at the promesonotal suture, but becoming feeble at their point of confluence. Fore wings with a short open radial cell. Hind wings veinless except for faint impressions at the base of the wing. Epinotum unarmed. Second node of petiole without ventral tooth, squamiform, broader and less constricted behind than in worker. Petiolar hairs sparse.

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